OBSERVATIONS ON THE TERTIARY FLORA OF AUSTRALIA, WITH SPECIAL REFERENCE TO ETTINGSHAUSEN'S THEORY OF THE TERTIARY COSMOPOLITAN FLORA.

Part II.

On the Venation of Leaves and its Value in the Determination of Botanical Affinities.

By Henry Deane, M.A., F.L.S., &c.

(Plates xxxv.-xxxviii.-xxxviii. *bis.*)

If a botanist, visiting a part of the world hitherto unexplored and failing to find the flowers or fruits of the plants occurring there, were to content himself with collecting leaves and thereupon to proceed to classify his specimens in natural orders and genera and to give them specific names, what would be thought of him? He might have ardently devoted himself to the task of collecting, have exposed himself to hardships and dangers in so doing, and he might have spent months or years at the work of classifying and describing his collection, and publishing his results, but in the end what would be the value of all his labours? To say the least of it, he would only earn ridicule if he were spending his own money; if, on the other hand, his expenses were provided by others, he would be scouted as an impostor, and he would run great risks of being put either into a gaol or a lunatic asylum. Yet it is difficult to distinguish this method from that adopted for the most part by palæontologists in dealing with fossil leaves. It is very rarely that fruits are found, and when they are, the structure is to a large extent obliterated, so that leaves are almost entirely depended on. Thousands of species have been created and their affinities declared on the evidence afforded by leaves alone, and often with an imperfect knowledge of the existing flora of the region and a preconceived desire to prove a certain theory.

The character of leaf-venation would prove an unerring guide to the determination of fossil plants if those characters were arranged through the vegetable kingdom on any orderly plan. If the leaves of all plants of a particular natural order possessed a common general character, and if those characters became more more defined and specialised as the genera were dealt with—if, finally, the specific differences were less than the generic differences, and still less than those of the ordinal differences, leaves would be as important a guide in the work of botanical classification as the parts of the flower, and the value of any particular fossil leaves would only depend upon the perfection of their preservation, as the affinities of those in which the substance and venation remain intact could then be absolutely determined.

One does not need to go far through the vegetable kingdom to find that leaves are not constructed on this methodical system, and almost immediately it will be recognised that not only do the leaves of different species of the same genus often differ very greatly from one another, but that their venation seems to be laid out on a totally different principle. On the other hand, leaves constructed on the same pattern and often undistinguishable are to be found in widely different natural orders.

The wonderful amount of variation in leaf-venation is a subject to which due weight is not always given, and those who are not botanists, but yet scientific men, can scarcely be blamed if they have been led to suppose that the structure of leaves has more or less followed in its development the general scheme of the higher divisions of the vegetable kingdom. The use of such specific names as "quercifolia," "ilicifolia," "acerifolia," "cinnamomifolia," &c., tend, at least, to give rise to the impression that the leaves of the various species of oak, holly, maple, cinnamon, &c.,

have at least something in common, even if they are not made on exactly the same plan; whereas those names refer only to the common species with which we from our childhood have been familiar. Even the genus *Acer*, most of the species of which have leaves constructed on the palmate or five-lobed pattern, shows very considerable variation; while the leaves of the different species of the genus *Quercus* show innumerable varieties of design, so great a divergence, indeed, that without following them through all gradations and intermediate links it might be wondered whether they could ever in the past have originated in one ancestral stock. The leaves of the same species seem occasionally to be made on a different pattern, as, for example, in *Q. aquatica*, a North American species, where in some cases the lateral or secondary veins run out to the margin of the lamina and terminate in teeth, while in other varieties they do not reach the margin at all, which is entire, but become lost in the general reticulation. *Q. cinerea* is another example.

The genus *Quercus* furnishes an excellent example of leaf-variation, and I have taken the opportunity of offering a number of examples for illustration. The genus is one which at the present day is widely distributed and which is, according to Ettingshausen, responsible for a great many of the fossil forms found in the Miocene beds of Australia. It, therefore, possesses a special interest. The number of species known to the authors of the "Genera Plantarum" and recognised by them is 300. In Plate xxxv. a sufficient number are figured to prove the great variety of types. As before mentioned, *Q. aquatica* and *Q. cinerea* show great varieties within the species. Reference may be made to Ettingshausen's* *Beiträge zur Tertiarflora von Java*, where remarkable variations of these two species are figured.

I have tabulated below the variations shown in Plate xxxv., grouping the leaves first, according to their shape; secondly, according to the character of the secondary veins; thirdly, according to the tertiary system. The texture of the leaf, whether mem-

* Sitzungsbericht der K. Akad. der Wissensch. 1 Abth. 1883, Vol. 87.

branous or coriaceous, flat, convex or with recurved margins, might also be used as a basis of classification. It may be seen that as all these different characters pass into one another by almost imperceptible gradations, there might be tabulated an enormously large number of combinations sufficient to include most dicotyledonous leaves, provided only that digitate, palmate and penniveined leaves are excluded.

SHAPE—

Entire—ovate, obtuse	*Q. elliptica.*
,, obovate	*Q. Phellos.*
,, ovate, lanceolate	*Q. lancifolia.*
,, ,, ,,	*Q. amherstiana.*
,, ,, ,,	*Q. fenestrata.*
,, broadly ovate, lanceolate	*Q. philippinensis.*
Serrate, regularly not deeply lanceolate	*Q. oxyodon.*
,, irregularly lanceolate	*Q. pseudococcifera.*
,, ,, ,,	*Q. lancifolia.*
Irregularly toothed, broadly ovate	*Q. alnifolia.*
,, ,, ovate	*Q. suber.*
,, ,, ,,	*Q. coccifera.*
Coarsely toothed, lanceolate	*Q. castaneæfolia.*
,, ,, ovate	*Q. Xalapæ.*
Regularly toothed, cuneate	*Q. Libani.*
Coarsely sinuate-toothed, rhomboidal	*Q. coccinea.*
Crenate, ovate	*Q. montana.*
Deeply crenate	*Q. Prinos.*
Irregularly lobed, rhomboidal	*Q. sessiliflora.*
,, ,, ,,	*Q. pedunculata.*
,, ,, to ovate	*Q. stellata.*
Deeply sinuate, with crenate lobes	*Q. pubescens.*

SECONDARY VEINS—

More or less straight, running to margin	*Q. castaneæfolia.*
,, ,, ,,	*Q. Libani.*
,, ,, ,,	*Q. suber.*
,, ,, ,,	*Q. Prinos.*
,, ,, ,,	*Q. montana.*
,, ,, ,,	*Q. Xalapæ.*
,, ,, ,,	*Q. pseudococcifera.*
Wavy and reaching margin	*Q. lancifolia.*

Wavy and reaching margin	*Q. stellata.*
,, ,, ,, ...	*Q. coccinea.*
,, ,, ,, ...	*Q. pedunculata.*
Curved and reaching margins	*Q. oxyodon.*
,, ,, ,, ...	*Q. alnifolia.*
Curved and reaching the next above	*Q. amherstiana.*
,, ,, ,, ,, ...	*Q. philippinensis.*
Curved and indistinct towards margin	*Q. elliptica.*
,, ,, ,, ,, ...	*Q. Phellos.*
Irregular and indistinct...	*Q. virens.*

Tertiary Veins—

At right angles to secondary, or nearly so.........	*Q. castaneæfolia.*
,, ,, ,, ,, ...	*Q. oxyodon.*
,, ,, ,, ,, ...	*Q. amherstiana.*
,, ,, ,, ,, ...	*Q. Libani.*
,, ,, ,, ,, ...	*Q. Prinos.*
,, ,, ,, ,, ...	*Q. Xalapæ.*
,, ,, ,, ,, ...	*Q. pubescens.*
,, ,, ,, ,, ...	*Q. montana.*
,, ,, ,, ,, ...	*Q. alnifolia.*
,, ,, ,, ,, ...	*Q. suber.*
At right angles to midrib	*Q. philippinensis.*
,, ,, ,, ...	*Q. lancifolia.*
Reticulate, but more or less arranged in lines ...	*Q. sessiliflora.*
Coarsely reticulate	*Q. stellata.*
,, ,, ...	*Q. coccinea.*
More finely reticulate	*Q. oloides.*
,, ,, ...	*Q. pseudococcifera.*
,, ,, ...	*Q. Phellos.*

In Plate xxxvi. I give some illustrations of leaves of the genus *Eucalyptus*, showing the remarkable variation in structure existing in the leaves of different species. Probably there are few people in Australia who would not express themselves sure of recognising a "gum tree" leaf when they saw it; they might even feel themselves insulted if doubt were expressed as to their power of doing so, and yet it is quite clear they could not express off-hand their idea of the typical *Eucalyptus* leaf. It may be a surprise to many to find on what different plans the vein system of the leaves of different species is arranged, and how impossible it is to pick out any one variety and say that is the *Eucalyptus* type. The secondary veins afford a great many different varieties. Observe for instance :—

E. coriacea and *E. stellulata* with their longitudinal veins; *E. Siberiana* and others with secondary veins placed at an acute angle with the midrib.

Follow the series down till the secondary veins become almost transverse.

E. microcorys, unlike most Eucalypts, has quite thin leaves.

The shape of the leaves might be thought to be fairly uniform and that they would all fall under the description of linear, lanceolate, acuminate, more or less falcate, and oblique at the base. All these characters break down in some of the specimens. Then it has been supposed that the intramarginal vein would be a pretty sure guide. It is, however, found in *Myrtaceæ* generally, in some *Proteaceæ*, in many *Apocynaceæ*, in many species of *Ficus*, and in genera belonging to many other natural orders. It is further to be remarked that in *Eucalyptus* itself its position is very variable, so that while in some leaves it is a considerable distance from the margin, in others it is so close to the edge as to be barely distinguishable.

In Plate xxxvii. are shown various Australian representatives of the Natural Order *Laurineæ.* It will be seen that the *Cinnamomum* character is not confined to the genus *Cinnamomum*, and that the *Laurus* type of venation is exemplified in some of these Australian genera. The *Cinnamomum* type makes its appearance also in *Rhodamnia* (Myrtaceæ), *Mallotus* (Euphorbiaceæ) both figured in the plate. It is clear that if either of these were found in the fossil state, and especially if they were fragments only, they might easily be taken for *Cinnamomum.* The same remarks apply with equal force to certain leaf-forms of the genera *Smilax* and *Rhipogonum (Liliaceæ)* and to *Rhodomyrtus (Myrtaceæ).*

The similarity in structure between certain leaves of the Order *Proteaceæ* and others of the Order *Sapindaceæ* is very marked.

Compare *Cupania serrata*, *Harpullia alata* and *Akania Hillii* with *Xylomelum pyriforme*, *Lomatia ilicifolia*, *L. Fraseri* and *Orites excelsa.*

On the other hand, note the differences between different leaves of the same species, *Akania Hillii* (Pl. xxxviii. *bis*, figs. 5-8), and between the leaves of *Lomatia Fraseri* and *L. ilicifolia*, plants which have such a multitude of intermediate forms that it becomes difficult, if not impossible, at times to decide under which species specimens are to be grouped (Pl. xxxviii. *bis*, figs. 1-3).

The pinnæ of many of the Australian *Sapindaceæ* and the leaves of some Australian *Saxifrageæ*, and the pinnæ of others, correspond to a remarkable degree with those of certain species of *Quercus*, a fact which Ettingshausen has apparently overlooked.

The leaves of *Doryphora sassafras* and those of the toothed variety of *Atherosperma moschata (Monimiaceæ)* are built on the same plan as the toothed variety of leaves of *Myrsine variabilis (Myrsinaceæ)*. There is no one point in which they can be said to belong to a different type. A comparison of different leaves off the same plant of *Myrsine variabilis* affords an example of remarkable specific variation (Plate xxxviii., figs. 3-4).

As examples of leaves almost identical occurring in different Natural Orders, those of *Pennantia Cunninghamii* (*Olacineæ*) may be compared with *Villaresia Moorei (ib.)*, and what is still more remarkable the leaves of *Vitis sterculifolia* and *Endiandra discolor* (*Laurineæ*) show a resemblance even to the glands or domatia which exist in the angles formed by the secondary veins with the midrib.

Compare also *Helicia ferruginea* (*Proteaceæ*) with *Olearia argophylla* (*Compositæ*) in Plate xxxviii. *bis*, figs. 11-12.

There are innumerable other examples of leaves of different genera and orders being so much alike that it is impossible to distinguish them, but the above examples are perhaps sufficient to prove the fact of the existence of such similarities. While searching for the affinities of fossil leaves the difficulty is generally not in finding resemblances but in making a selection, as the resemblances are often so numerous.

Judging from a paper read by Ettingshausen before the Imperial Academy of Vienna in the year 1854,* no one could recognise the difficulties more than that author. In this paper he mentions how attention had been called to the subject of leaf venation two years before by Leopold von Buch at a meeting of the Berlin Academy of Sciences, and regret therein expressed that investigation with a view to classification of leaf characters had not been seriously attempted. Ettingshausen points out in his paper the impossibility of carrying out any systematic classification, and he mentions how the forms and venation of *Ficus* and *Vochysia*, *Cinnamomum* and *Strychnos*, *Mertensia* and *Ceanothus* or *Zizyphus*, *Fagus* and *Dipterocarpus*, *Salix* and certain *Lythrarieæ*, *Jacaranda* and *Mimoseæ*, *Nyssa*, *Diospyros* and *Pittosporum*, *Santalum* and *Sapotaceæ* entirely correspond. On the other hand, he shows how we come across the most heterogeneous types of leaves in one and the same natural order or even the same genus, as for example, in *Bignoniaceæ*, *Saxifrageæ*, *Büttneriaceæ*, *Euphorbiaceæ*, in *Ficus*, *Sterculia*, &c.

It would appear, therefore, that the matter scarcely calls for any argument seeing that this great authority in fossil leaf naming acknowledged at the outset how utterly unreliable leaf characters were as a guide to classification, and the only wonder is that after the recognition of the impossibility of adopting any system, these sensible conclusions should have been put on one side and the naming of fossil plants from leaves only and often from very badly preserved fragments should have been carried on in such a wholesale manner and with such confidence.

Ettingshausen has carried out a vast amount of investigation, some of which no doubt is very useful and of great interest, as, for instance, when he attempts to trace back the genealogy of *Castanea vesca* to *C. atavia*. This is a kind of work which is

* On the *Euphorbiaceæ*: Sitzungsber. der K. Akad. der Wissensch. Band xii.

sound in principle, when it consists in comparing fossil remains from successive horizons with existing plants growing in the same or in contiguous regions, but it is quite a different thing when the attempt is made to prove that certain fossil forms belong to groups non-existent in this particular part of the world and found on the other side of the equator, and perhaps in another hemisphere.

EXPLANATION OF PLATES.

Plate xxxv.

Fig. 1.—*Quercus elliptica.*
Fig. 2.— „ *Phellos.*
Fig. 3.— „ *aquatica.*
Fig. 4.— „ „
Fig. 5.— „ „
Fig. 6.— „ *lancifolia.*
Fig. 7.— „ „
Fig. 8.— „ *amherstiana.*
Fig. 9.— „ *fenestrata.*
Fig. 10.— „ *philippinensis.*
Fig. 11.— „ *oxyodon.*
Fig. 12.— „ *suber.*
Fig. 13.— „ *alnifolia.*
Fig. 14.— „ *pseudococcifera.*
Fig. 15.— „ *castaneæfolia.*
Fig. 16.— „ *Libani.*
Fig. 17.— „ *Xalapæ.*
Fig. 18.— „ *coccinea.*
Fig. 19.— „ *Prinos.*
Fig. 20.— „ *montana.*
Fig. 21.— „ *sessiliflora.*
Fig. 22.— „ *pubescens.*

Plate xxxvi.

Fig. 1.—*Eucalyptus coriacea.*
Fig. 2.— „ *stellulata.*
Fig 3.— „ *Sieberiana.*
Fig. 4.— „ *amygdalina.*
Fig. 5.— „ *obliqua.*
Fig. 6.— „ *pilularis.*
Fig. 7.— „ *microcorys.*

Fig. 8.—*Eucalyptus polyanthema.*
Fig. 9.— ,, ,,
Fig. 10.— ,, *paniculata.*
Fig. 11.— ,, *populifolia.*
Fig. 12.— ,, *largiflorens.*
Fig. 13.— ,, *longifolia.*
Fig. 14.— ,, *maculata.*

Plate xxxvii.

Fig. 1.—*Cinnamomum Burmanni.*
Fig. 2.— ,, *Tanala.*
Fig. 3.— ,, *Oliveri.*
Fig. 4.—*Cryptocarya triplinervis.*
Fig. 5.— ,, *cinnamomifolia.*
Fig. 6.— ,, *australis.*
Fig. 7.— ,, *microneura.*
Fig. 8.— ,, *obovata.*
Fig. 9.—*Litsæa hexanthus.*
Fig. 10.— ,, *dealbata.*
Fig. 11.—*Endiandra glauca.*
Fig. 12.— ,, *Muelleri.*
Fig. 13.— ,, *pubens.*
Fig. 14.—*Rhodamnia trinervia.*
Fig. 15.—*Mallotus philippinensis.*

Plate xxxviii.

Fig. 1.—*Doryphora sassafras.*
Fig. 2.—*Atherosperma moschata.*
Fig. 3.—*Myrsine variabilis.*
Fig. 4.— ,, ,,
Fig. 5.—*Pennantia Cunninghamii.*
Fig. 6.—*Villaresia Moorei.*
Fig. 7.—*Vitis sterculifolia.*
Fig. 8.—*Endiandra discolor.*

Plate xxxviii. *bis.*

Fig. 1.—*Lomatia ilicifolia.*
Figs. 2-3.—*Lomatia Fraseri.*
Fig. 4.—*Orites excelsa.*
Figs. 5-8.—*Akania Hillii.*
Figs. 9-10.—*Cupania serrata.*
Fig. 11.—*Helicia ferruginea.*
Fig. 12.—*Olearia argophylla.*